CHAPTER 18

Slippin' and slidin' between the scales: the scaling components of biodiversity–ecosystem functioning relations

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18.1 Introduction

Whilst the problems of scale are well-known to most ecologists, many subdisciplines of ecology are still struggling with its central concepts—how the dimensions of space and time, and levels of organization, influence ecological patterns and processes (e.g. Peterson and Parker 1998; O'Neill and King 1998; Petersen and Hastings 2001; Schneider 2001). Individual ecologists may, at their own peril, ignore the problem and focus on one scale and one level of organization only. However, the synthesis of many individual studies conducted at different scales requires a better understanding of the influence of scale on ecological processes. This is particularly evident in the study of biodiversity and ecosystem functioning. Although studying at least two levels—community and ecosystem—most research has been performed at small spatial and short temporal scales (Loreau *et al.* 2001; Naeem 2001), and it is not clear if such studies can be used to inform the public and policymakers about the large-scale consequences of biodiversity loss.

An example of the small spatio–temporal scales often used in biodiversity–ecosystem functioning studies are the grassland experimental plots, which have formed the core of the recent examinations of such relationships. These plots usually have a spatial extent of $<100\,m^2$ and the experiments span a period of a few to ten years (<1 to 10 generations depending on the species) (Hector *et al.* 1999; Tilman *et al.* 1996, 1997a). Similarly, microcosm experiments are by definition small in space in comparison to the systems they are modelled after, such as using Ehrlenmeyer flasks as model fresh-water ecosystems (McGrady-Steed *et al.* 1997; Naeem and Li 1997). However, microcosms can encompass a large number of generations for small organisms such as prokaryotes, protists, or other members of phytoplankton and zooplankton communities, and can have a large spatial scale relative to the organisms concerned (see Petchey *et al.*, Chapter 11).

A second major issue regarding scale and biodiversity–ecosystem functioning research is that most experiments carried out so far have been more or less closed to their surroundings. This precludes processes varying at larger spatial scales from influencing the results, leaving only local interactions to determine community composition and diversity. In systems where disturbances and landscape configuration strongly influence diversity and community structure, such small-scale experiments may only reveal part of the story.

The term 'scale' usually refers to dimensions of observed entities and phenomena in space and time (i.e. extent, grain, size and resolution; O'Neill and King 1998; Schneider 2001). Scale does not describe the level of organization of a system (populations, communities, and ecosystem), although scale is

sometimes referred to in this context. Populations or ecosystems have no general scale, although specific systems may have dynamics on particular scales in relation to organism size and generation time. Naeem (2001) uses the ambiguous term 'biotic scale' for genetic, population and ecosystem properties, admitting that these lack standard units for measurement and that these operational units vary among studies. When the scale of investigation changes properties of communities and ecosystems do not just change in any coherent fashion. That is, if one investigates a large-scale phenomenon using a small-scale experiment, or conducts an experiment for two generations to study a phenomenon that occurs on a scale of 10 generations, there is seldom any justification in the assumption that one just has to multiply up or down to make predictions about the phenomenon from experimental results. Rather, the extrinsic and intrinsic forces driving the dynamics of populations or ecosystems may change (O'Neill and King 1998). A well-known example from population dynamics is metapopulation dynamics (e.g. Hanski 1999). Resource competition or predation may determine local-dynamics, but at the regional scale patch relationships, landscape configuration and dispersal are more important.[1]

Not only do ecologists struggle with space–time scaling problems in their attempts to understand relationships between communities and ecosystems, but they must also take into account the various degrees of artificiality imposed on study systems by their experiments (Naeem 2001; Fig. 18.1). It is well known, for example, that enclosures and exclosures impose artificial boundaries on the study systems. This creates edge effects on dynamics that may seriously confound the interpretation of results from such studies (e.g. Peterson and Hastings 2001). Theoretical approaches, model systems like microcosms, experiments on plots in the field, and natural ecosystems have their own space–time domains. How to extrapolate from, for example, theory to protist microcosms to freshwater pond or temporary pool ecosystems to larger major ecosystems, such as lakes or forests, is not clear at all. In addition, within each space–time–artificiality domain, ecologists can study populations, communities or ecosystems, or combinations of these levels (Fig. 18.1). This adds further complication, because studies at one level of organization may not be directly relevant at other levels, even if performed at the same scale.

Given this multiplicity of scales and levels of organization, there are some central questions that must be tackled (e.g. Levin 1992, 1999; Anderson 1995; Peterson and Parker 1998; Loreau 2000a; Petersen and Hastings 2001; Gardner *et al.* 2001) if we want to improve our understanding of the nature and functioning of ecosystems:

- How do we know that what we learn at one scale and level is relevant at other scales?
- How do we (and can we) extrapolate to other scales?
- Can we generalize diversity effects on ecosystem functioning across different ecosystems and scales?
- What are the perils when ignoring scaling issues?

An additional question, especially important as ecologists are increasingly asked to provide information for policy-makers, is:

- Do the studies we conduct at smaller scales inform us about the consequences of biodiversity loss at the landscape and regional scales that policy-makers are most interested in?

In this chapter, we discuss these scaling questions in the context of studies on biodiversity and ecosystem functioning. We place special emphasis on the relationship between studies of local within-site dynamics and regional (landscape) dynamics, and consider the extent to which we can scale up from local plots to landscapes, from the laboratory to the field, and from artificial to natural systems.

[1] In this chapter, our use of the terms landscape and region are context-dependent. When discussing diversity and dynamics of populations and communities, we use 'regional' as an opposite to 'local', e.g. regional metapopulation dynamics versus local within-patch dynamics. However, when referring to spatial scales, we use landscape as an intermediate scale, larger than local but smaller than a geographic region, encompassing several habitats, and to a large degree defined by human perception. It is only from a human perspective that the landscape scale makes good sense, and hence model systems with model landscapes (see below) may not necessarily be relevant for our management of ecosystems.

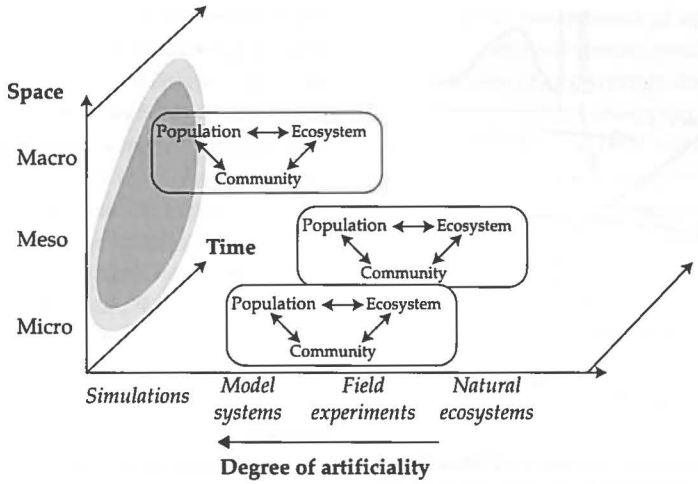

Figure 18.1 Ecological studies can be made at many combinations of scales in space and time, degrees of artificiality, and on several levels of organization. Studies made in one space–time–artificiality domain are not necessarily relevant in other domains and other levels. Experimental studies on diversity and ecosystem functioning have mainly been made in a small subset of the possible space–time–artificiality combinations (mainly model systems and field experiments as indicated; e.g. McGrady-Steed *et al.* 1997; Naeem and Li 1997; Laakso and Setälä 1999b; Tilman *et al.* 1996, 1997; Hector *et al.* 1999), while simulations seem most relevant in a different domain of long time scale but undefined spatial scale (e.g. Norberg *et al.* 2001). In all cases, diversity–ecosystem functioning studies have studied the linkage between population/community and ecosystem levels. (Modified after Naeem 2001)

18.2 Relating local plot experiments to regional patterns

One of the sources of controversy in the biodiversity debate has been the conflict between the results of small-scale experiments and comparative multi-site studies (Loreau *et al.* 2001). Take for example the relationship between productivity and diversity. This relationship is often described in the literature by a hump-shaped curve, with peak diversity at some intermediate level of productivity (Fig. 18.2, small graph). A large number of mechanisms have been posited to explain why diversity depends on productivity, but no single explanation seems to have unequivocal support (Rosenzweig and Abramsky 1993; Huston 1994; Abrams 1995a).

The first approach taken in most examinations of this relationship compare diversity between sites with different primary productivity or other variables, e.g. nitrogen availability, that indirectly indicates productivity. The second approach is that of the more recent experiments on the effects of diversity on ecosystem functioning (Naeem *et al.* 1993; Tilman *et al.* 1996, 1997a; Hector *et al.* 1999, Chapter 4) that have turned the diversity–productivity question on its head (Loreau *et al.* 2001; Fig. 18.2). Here diversity is suggested to be one of the factors that productivity depends on. Experiments examining this hypothesis manipulated diversity at single or several sites on which there was no perceived variation in other factors affecting productivity, such as water or nitrogen availability.

This second approach, in which productivity is the response or dependent variable rather than the independent variable as in the first approach, examines whether variation in diversity affects productivity within sites, keeping other factors constant. This corresponds to experimentally varying diversity at a particular potential productivity, but should not be confused with between-site comparisons. One way of reconciling the results from the two approaches is to superimpose the results of the recent experiments on the area defined by the hump-shaped curve (Fig. 18.2, large graph) (Lawton 2000; Loreau *et al.* 2001). The experiments could be interpreted as examining whether a local decrease

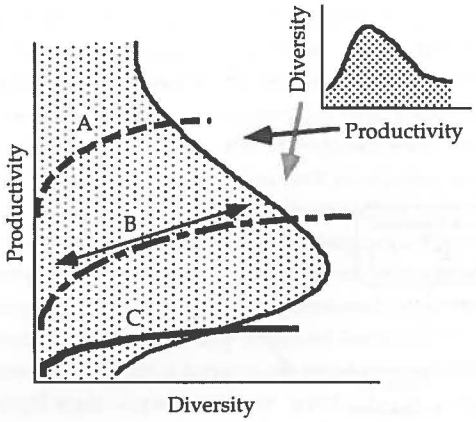

Figure 18.2 The two approaches to the relationship between diversity and plant biomass productivity examine different questions. In one approach, the relationship between productivity and local diversity is usually described by a hump-shaped boundary line, with a large number of data points in the area underneath this line (small graph). This approach mainly attempts to explain large-scale (between site) variation in diversity by factors such as productivity, climate or disturbance regime. Recent experiments on biodiversity and ecosystem function turn this question around and examine if variation in diversity at single sites affects productivity, keeping other factors constant. If the axes are switched, these experiments can be viewed as examining the trajectory of productivity response as diversity is experimentally decreased (or increased) at a single site (large graph; A, B, and C indicates three sites with different potential productivity, the arrow indicates how species richness can be varied). (Modified after Lawton 2000 and Loreau *et al.* 2001)

in diversity reduces the ability of a community to realize the potential productivity of a site. Such decreases in local diversity may arise from either local or regional processes, such as changes in management and land use, or habitat fragmentation.

It should have been clear from the start that these two approaches are different for two reasons. Firstly, the humped curve of productivity versus diversity is actually a boundary with a large amount of data points filling the space underneath, rather than a single line (Fig. 18.2, small graph).[2] At any point, species can be removed, species composition manipulated, or nutrients added or removed. The ensuing effects can then be examined as a trajectory in the graph. Consequently, the first approach, in which diversity is the response variable, attempts to explain larger-scale variation in diversity, which may depend on productivity (resource availability) but also on many other factors such as disturbance regime, spatial heterogeneity, climate or herbivory. Secondly, what is meant by 'productivity' often differs. In some instances, productivity refers to the site fertility, energy inputs, water regimes, or other extrinsic factors, while in other instances 'productivity' refers to the activity, such as biomass production or nutrient cycling rates, of the community at the site. Clearly an ecosystem's functioning is affected by both productivity in terms of extrinsic factors as well as intrinsic, or biotic factors such as what species are there, the relative abundance of these species, and how they interact with one another.

Can results from small-scale local plot experiments be extrapolated to larger scales and inform us about the consequences of biodiversity loss at the landscape or regional scales? Under special circumstances, the answer can be 'Yes!'. When the drivers[3] of productivity and diversity are the same at the different scales, small-scale experimental studies will also shed light on patterns at larger scales. However, if the drivers are different, then the extrapolation is not valid, and studies addressing the landscape or regional scale are required for answering questions at this scale (O'Neill and King 1998).

From the field experiments of Hector *et al.* (1999) and Tilman *et al.* (1996, 1997a), three mechanisms emerged as potential candidates to explain the patterns between diversity and productivity these studies observed—complementarity, positive interactions, and sampling effects. All act primarily at small spatial scales. The former two are local deterministic explanations for both increased diversity and increased productivity based on niche partitioning theory. The three mechanisms are based on the assumption that species interactions and the functional traits of species drive the relationship between diversity and ecosystem functioning. However, on larger scales and when comparing the same local habitat type across space, variation in productivity and other ecosystem processes is mainly caused by variation in resource availability

[2] We owe this point to B. Schmid.

[3] In the following, we use the term 'driver' as a convenient abbreviation for 'factors or mechanisms explaining variation in community or ecosystem characteristics such as diversity or productivity'.

and abiotic factors (Huston 1994; Anderson 1995). At the same time, factors other than niche partitioning drive diversity at larger scales, e.g. dispersal and propagule production, disturbances, and spatial patterns in environmental factors can all regulate biodiversity. This suggests that many small-scale experiments may be of limited relevance for understanding biodiversity–ecosystem functioning relations on larger scales, unless they incorporate spatial and temporal heterogeneity, disturbances, or dispersal limitation of species in the experimental design, and possibly also other extrinsic drivers of biodiversity.

At local sites, positive effects of diversity on ecosystem processes such as productivity and nutrient mineralization are most likely to be found when the process as well as the maintenance of diversity are linked to resource utilization and availability, and mechanisms such as complementarity, positive interactions, and competition operate. However, not all local ecosystems are dominated by these factors and biotic or interaction-based mechanisms. In early successional systems that are strongly affected by frequent disturbances, the relationship between diversity and ecosystem functioning may be very different. Because resource limitation is not strong under such conditions and dispersal has a large stochastic component, local productivity patterns may be driven by the traits of colonizers and dominant competitors in earlier stages of succession, yielding little or no effect of diversity on ecosystem functioning. Engelhart and Ritchie (2001) suggested that disturbances in wetlands might allow less competitive species with strong effects on ecosystem processes to coexist with competitively superior species. Because competitive dominants with lower productivity form largely monospecific stands in the absence of disturbances, plant diversity needs to be increased to enhance ecosystem functioning. In this case, the mechanism is related to the interaction between disturbance regime and competition, rather than niche partitioning. Loreau and Mouquet (1999) pointed out that when diversity is maintained by immigration, productivity should on an average stay constant or decrease with increases in diversity.

Regional diversity losses could, however, decrease local productivity in systems where productivity depends on recruitment of appropriate dominants from the regional species pool after disturbances. If populations of appropriate dominants for local sites become too rare or disappear regionally, the potential productivity of local sites may not be realized because dominants, assumed to be most efficient in production, colonize too slowly or not at all. The trade-off between competitive and colonization ability (e.g. Levins and Culver 1971; Hanski and Ranta 1983; Nee and May 1992; Yu and Wilson 2001), suggests that this may result in greater losses of competitive species with strong effects on ecosystem processes (e.g. Tilman *et al.* 1994). Thus, plant communities in fragmented landscapes may increasingly consist of species with traits enhancing dispersal and rapid colonization, rather than species with traits leading to high competitive ability, such as the ability to deplete soil resources that may enhance nutrient retention (assuming that competitive abilities and dispersal represent trade-offs in organisms). This change in biodiversity–ecosystem functioning is just one consequence of larger and larger areas becoming part of 'a weedy world'.

18.3 The degree of similarity across ecosystem types in diversity–ecosystem functioning relationships

If we move from local plots to landscapes, our study area may include more and more ecosystem types (grasslands, forests, lakes, river banks, etc). This leads to a second controversy in diversity–ecosystem functioning studies, which has been based on the fact that results from one ecosystem do not necessarily inform us about other systems. This is perhaps a trivial finding but nonetheless one that has often been overlooked when ecologists have entered the area of policymaking.

Most empirical studies on diversity-functioning relationships have been conducted in mesic grasslands. Is there any reason to expect that other ecosystems would behave differently? Studies in other systems both support and contradict the mesic grassland studies. The majority of experiments do indeed show some relationship between species diversity and functioning, usually at the low end of the diversity gradient (Schwartz *et al.* 2000), but there are some notable exceptions. Even in grasslands,

single functional groups can outperform functional group mixtures, and Troumbis *et al.* (2000) observed an inverse sampling effect, in which superior competitors do not have the greatest effect on ecosystem processes (Loreau 2000a). Engelhart and Ritchie (2001) also observed such an effect in wetlands.

Studies of soil systems have yielded little support for effects of species diversity in soils on decomposition and production, although several experiments clearly show that functional diversity of soil fauna increases nitrogen mineralization and plant growth (e.g. Laakso and Setälä 1999b; Hooper *et al.* 2000; Mikkola *et al.*, Chapter 15; Wardle and van der Putten, Chapter 14). Also, soil process rates seem to be more affected by the properties of individual plant species, e.g. litter chemistry, than by plant diversity (Wardle *et al.* 1997a; Wardle and van der Putten, Chapter 14).

It may be too early to conclude that there is any consistent variation in the shape and existence of diversity–ecosystem functioning relations among major ecosystems or ecosystem processes. Before we, as ecologists, are in a position to be able to start making scientifically robust predictions on these relationships, there is an enormous amount of research necessary that is difficult in both its extent and complexity. Figure 18.3 outlines some basic requirements (see also e.g. Bengtsson 1998; Schläpfer and Schmid 1999).

Starting from the (hitherto) paradigm system 'mesic grassland plant diversity and productivity', there are a number of avenues for further studies. We can examine the effects of primary producer diversity (or microbes in decomposition systems) on production in a variety of ecosystems, such as forests, soils, lakes, streams, etc. We can also begin

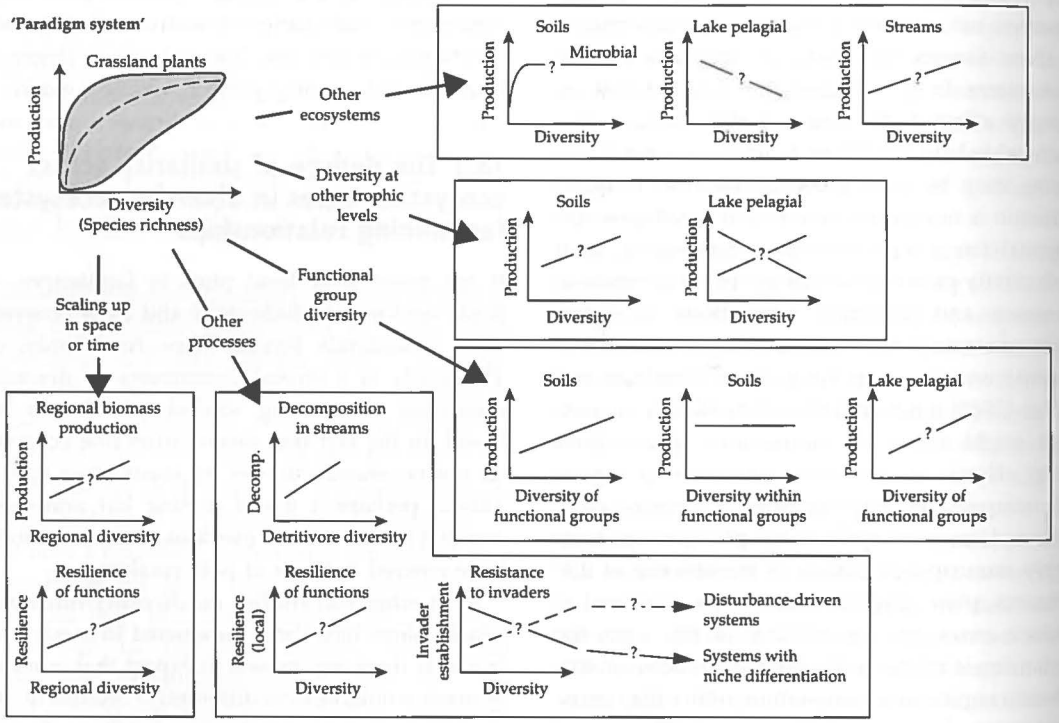

Figure 18.3 Studies on biodiversity and ecosystem functioning have been made on a small number of ecosystems, ecological levels, and scales. The major 'paradigm study system' has been plant biomass production and species diversity in mesic grasslands (e.g. Tilman *et al.* 1996, 1997; Hector *et al.* 1999). These studies should be complemented with studies (a) in other ecosystems, (b) manipulating diversity at other trophic levels, (c) manipulating the diversity of functional groups, (d) examining other ecosystem processes, and (e) at larger scales than local plots or sites. The panels in the figure give some examples of such complementary studies that are needed. Hypothetical relationships between diversity and ecosystem functioning are indicated (based on studies referred to in the text). See also text for explanation.

to study systems where higher trophic levels may affect diversity (Paine 1966; Connell 1975), production (e.g. Setälä and Huhta 1991; Laakso and Setälä 1999b; Wedin 1995) and the shape of the relation between primary producer diversity and production (Mulder *et al.* 2000). It would hence be highly appropriate for future studies to incorporate diversity at higher trophic levels (see Raffaelli *et al.*, Chapter 13). How we treat the diversity of functional groups (Hooper and Vitousek 1997; Tilman *et al.* 1997; Hector *et al.* 1999; Laakso and Setälä 1999b) in a multitrophic system is particularly challenging.

The world does not consist of primary production alone. Other ecosystem processes of interest include other rate processes such as decomposition, nutrient mineralization and retention, and secondary production. In soils, decomposition and nutrient mineralization were positively related to the diversity of soil animal functional groups (Laakso and Setälä 1999b), while in streams decomposition was positively affected by the number of species (Jonsson and Malmqvist 2000), albeit at the low end of the diversity gradient.

We might also consider the effect of diversity on the stability of the systems, the variability (or conversely reliability) of ecosystem processes (see Loreau *et al.*, Chapter 7 and Hughes *et al.*, Chapter 8), the resilience of processes or of community composition, or invasion resistance (e.g. McGrady-Steed *et al.* 1997; Naeem 1998). Stability and resilience in most local ecosystems are likely to depend on an interplay between local and regional processes, with diversity as a key component (Holling *et al.* 1995; Petersen *et al.* 1998; Bengtsson *et al.*, in press; Levine *et al.*, Chapter 10). Finally, local relationships may or may not scale up to landscape or regional relations, so each system and process ought to be studied at several scales.

These short paragraphs have sketched a multidimensional problem with almost infinite possibilities for combinations of study objects. In spite of this, comparable studies of diversity-functioning relations in a number of different major ecosystems should be of high priority, with due considerations of the limitations that face almost any such study. The study of soil fauna effects on plant growth by Laakso and Setälä (1999b) is exemplary for addressing several of the dimensions at the same time—species and functional group diversity, several trophic levels and several processes. As we scale up in space and time, the issue of replication becomes a difficult one, and statisticians may well need to come to grips with issues of what constitutes statistically acceptable designs in the face of pragmatic and realistic experimental constraints in a variable world.

In the absence of data and theory for many ecosystems and processes, what can ecologists say at this time about the expected relations between diversity and ecosystem functioning in different systems? Differences among studies, sites or ecosystems in the effects of diversity on ecosystem functioning are likely to be related to the major factors driving diversity, species abundance and process rates in different systems (Table 18.1). If resources are limiting, exploitative rather than interference competition dominates, and if the potential for partitioning of resources among species exists, then niche-based complementarity is a reasonable mechanism explaining a positive relationship between diversity and the rate of a process related to that resource (Loreau 2000a; Loreau and Hector 2001). Positive interactions among species that increase resource utilization or the amount of available resources would lead to similar positive relations.

However, in other circumstances these mechanisms may not be the driving factors, in which case the effects of species richness on ecosystem functioning may be relatively minor. This is nicely illustrated by contrasting the species diversity-invasion resistance results of Levine (2000a) for plant assemblages along rivers and McGrady-Steed *et al.* (1997) for protist microcosms. In McGrady-Steed's relatively homogenous and closed microcosms, where diversity was the only factor varying among treatments, diversity was found to enhance invasion resistance. Levine (2000a) found a similar effect of diversity locally, but in contrast, at the 8 km scale of his riparian system, factors other than diversity such as seed supply drove invasion success. This is not to say that diversity is inconsequential, but at community-wide scales in heterogeneous systems, the effects of diversity may be overwhelmed by other factors (see Levine *et al.*,

Table 18.1 Possible relations between diversity and ecosystem functioning (in general) in ecosystems with different driving forces (mechanisms) for diversity and process rates. Systems fulfilling conditions under A are expected to show a positive relation between diversity and ecosystem functioning locally, whereas systems under B are not, based on present knowledge. Functions under C and D are related to stability rather than process rates, C refers to local diversity, D to regional diversity

Systems	Expected effect of diversity on function	Mechanisms
A		
Systems with exploitative competition for limiting resources that can be partitioned	Positive	Complementarity, Niche partitioning
Systems with positive interactions between species (mycorrhiza, N-fixation)	Positive	Increased resource availability or amount of resources with diversity
B		
Disturbance-driven systems	No?	Growth rates and colonization rates of individual species drive functions (initially)
Top-down effects dominating	Positive, no or negative (?)	Consumers preclude resource partitioning, resource limitation may not occur
Interference competition dominates	No or negative?	Traits of dominants drive function
Processes not resource-limited, or resources cannot be partitioned (examples: soil fertility, maintenance of atmospheric composition, etc)	No? unclear, or meaningless	Various
C		
Invasion resistance in systems with resource limitation and niche partitioning	Positive	No 'empty niches' available for colonizers
Invasion resistance in disturbance-driven systems	Negative	Disturbances enhance diversity and establishment of all species
D		
Resilience of functions: larger spatial and temporal scales, mosaic landscapes, disturbances, species substitutable, etc.	Positive (?)	Portfolio effect (spatial and temporal), spatial resilience, dispersal among patches possible, several species in functional groups provides redundancy

Chapter 10). More generally, we find it likely that in early successional plant systems establishment through dispersal from nearby patches and the traits individual species of colonizers, e.g. growth rates, will be more important than complementarity in driving ecosystem processes following the disturbance. How organism size and generation time relate to the diversity–ecosystem functioning relationship must also affect the relative importance of these mechanisms. The generation time in relation to disturbance frequency and organism size in relation to resource heterogeneity will produce variable responses even within similar ecosystems.

Some ecosystem processes are not resource-based and there may be no potential for resource partitioning to influence them. Examples may be soil fertility, maintenance of atmospheric composition, erosion control, and possibly resilience and resistance to disturbances. In the case of resilience, diversity may still be important because of other mechanisms (the insurance hypothesis, spatial resilience; see below) and at larger scales. Finally, positive effects of diversity on rates of ecosystem processes may be less common in systems where interference competition is strong and consequently only a few species are dominant. In this case, niche partitioning is not an important factor structuring the community.

Future empirical and theoretical studies should seek a more unified framework in which to place

the different types of diversity–ecosystem functioning results that may emerge. This would aid the process of generalizing from the present case by case nature of the subject. Figure 18.3 and Table 18.1 is a first attempt to develop such a framework, and it would be informative to be able to compare results from a number of studies of diversity-functioning relations in systems which differ according to the criteria in Table 18.1.

18.4 Regional diversity maintaining resilience and local ecosystem functioning

Environmental variation and disturbances are ubiquitous in ecosystems. Much of classical community ecology was developed from a perspective of local species interactions and succession at single sites. Disturbances, if they occurred, were viewed as small-scaled, and disturbed areas were assumed to be recolonized from within the local system. The surrounding landscape and its diversity was regarded to be of minor importance. However, theories of metapopulations and spatial dynamics, and the still undigested perspective from landscape ecology, are beginning to change the emphasis from the local to larger scales in many communities (some recent examples are Hanski 1999b; Lawton 2000; Nyström *et al.* 2000; Hubbell 2001; Bengtsson *et al.*, in press). Yet, studies of biodiversity and ecosystem functioning have been almost entirely performed within a fairly narrow scale paradigm emanating from classical (local) community ecology. If we want to answer questions about the consequences of biodiversity loss on larger scales than plots or microcosms, we need to incorporate insights from other perspectives emphasizing regional and landscape scales.

A growing number of studies across many different ecosystems suggest that local and regional diversity are related to each other, and that the surrounding landscape can have a profound impact on local communities (e.g. Srivastava 1999; Lawton 2000; Loreau 2000a,b; Bengtsson *et al.*, in press). A recent review by Lawton (2000; but see Loreau 2000b) suggests that local communities may be arranged along a continuum from those that are proportional samples from the regional species pool to those in which species interactions sets limits to species richness. In the former systems (termed 'type I systems'), processes driving regional diversity should be particularly important for local diversity. For example, the disappearance of species in intensively managed landscapes as a consequence of the ongoing landscape fragmentation and habitat loss will affect the diversity and abundance of those species that remain (Bascompte and Rodriguez 2001). This could have effects on important ecosystem services such as biological control. In fact, in agroecosystems Thies and Tscharntke (1999) and Östman *et al.* (2001) showed substantial effects of landscape heterogeneity on biological control by parasitoids and generalist predators, respectively. In both cases, biological control was more efficient in small-scaled heterogeneous landscapes. A similar case might also be made concerning pollinator declines because of fragmentation (e.g. Buchman and Nabhan 1996; Thomson 2001).

In ecosystems where disturbances are frequent and regional species composition is important for local communities, ecosystem reorganization after disturbances will be affected by both local conditions and the landscape composition in the surroundings of disturbed patches (Holling *et al.* 1995; Bengtsson *et al.*, in press). Important local factors affecting ecosystem reorganization after disturbances include seed banks, structures allowing recolonization (often termed 'biological legacies'; Turner *et al.* 1998; Franklin and MacMahoon 2000) and species interactions during succession. The surrounding landscape, on the other hand, contains the areas that serve as source patches for propagules, the species that transport propagules, and species that interact and interfere with the dispersal, dynamics and succession in local patches (Bengtsson *et al.*, in press). This was termed 'spatial resilience' by Nyström and Folke (2001), and the processes are likely to be important no matter the shape and existence of a relation between diversity and rate processes. The composition of the landscape will affect the recruitment of the dominant species locally driving ecosystem processes during earlier stages of succession, and the recruitment of appropriate species to fill 'local niche space' and increase local resource utilization through increased

diversity. Landscape composition will also influence the modification of the diversity–ecosystem functioning relations through redistribution of water, soil particles and seeds, and interactions between vegetation and higher trophic levels. Species at higher trophic levels are more likely to have large home ranges and their dynamics depend on landscape composition at larger scales than local patches (e.g. Ritchie and Olff 1999).

One larger-scale perspective on the relation between diversity and ecosystem functioning that might be useful to incorporate in future studies comes from island biogeography and metapopulation dynamics. For example, species-area relations imply that the long-term maintenance of local diversity at a given level may require much higher diversity at regional scales (Tilman 1999b). The mechanism is the classical one—local extinctions must be balanced by new colonization events from the species pool for diversity to be maintained (MacArthur and Wilson 1967). However, in the original island biogeography theory, the species pool on the mainland is constant and not affected by the islands in question (but see Schoener 1976). In mainland systems, however, the species pool is continually produced by the component local communities sending dispersing propagules to other patches. Changes in local community composition, in particular directional ones such as abundance declines and extinctions, will sooner or later feed back to produce the new regional species pool. Hence, if the temporal scale is extended, regional diversity and species composition is a dynamical variable in real ecosystems (Hubbell 2001). Systems with this kind of dynamics were modelled by Wilson (1992), but have received relatively little attention from theoreticians and empirical ecologists.

Another perspective is the body of theory developed by Holling and co-workers about multiple stability domains in ecosystem dynamics (e.g. Holling *et al.* 1995; Petersen *et al.* 1998; Gunderson 2000; Scheffer *et al.* 2001). This theory differs somewhat from much of textbook theoretical community ecology in its emphasis on multiple stable states in ecosystems, and how transitions between the states are produced. For Holling and co-workers, ecological resilience is the magnitude of disturbance that an ecosystem in one stability domain can absorb (resist) before it moves into another stability domain (Gunderson 2000).[4] Biodiversity is assumed to play a key role in this respect (Holling *et al.* 1995; Walker *et al.* 1999), because losses of biodiversity are regarded as making systems more vulnerable to disturbances that move them into new stability domains (Scheffer *et al.* 2001).

The consequences of this theory are related to the ecological redundancy and its role in insuring ecosystem functioning (e.g. Naeem 1998; Walker *et al.* 1999), but extended from local to larger scales. For an ecosystem to reorganize, i.e. remain within the same stability domain, after a disturbance, a diversity of species and structures within the disturbed area and in the surrounding landscape is needed. Ecosystem functions, being performed by species, are maintained in large-scale mosaic systems if a number of species exist that are to a large degree substitutable (Walker *et al.* 1999). Such substitutable species are regarded as being able to coexist in the landscape primarily because they have dynamics at different scales in space and time (Petersen *et al.* 1998; see also Ritchie and Olff 1999). In this way, they contribute to the resilience of the system even though they may appear to play no functional role at the moment. Ecosystem resilience is maintained in the long term by preserving biodiversity on the landscape and regional scales (Holling *et al.* 1995; Petersen *et al.* 1998; Bengtsson *et al.*, in press).

Another component of the Holling theory is the adjustment of ecosystems and the functions performed in them to environmental changes (termed ecosystem adaptation by the proponents of the theory). When regional diversity is high, there will be not only many substitutable species, but also many species with different traits and requirements. For example, if spatial heterogeneity is maintained in managed landscapes, species with different niches can coexist more easily. When landscapes are subjected to environmental changes, such as global warming or decreased rainfall, a high regional diversity would allow ecosystems to adjust to these changes more easily by recruiting the appropriate species from the species pool, thus maintaining

[4] Note that Holling's 'ecological resilience' is termed 'robustness' in Loreau *et al.*, Chapter 7.

ecosystem functioning (Norberg *et al.* 2001; Chapter 7). If this is true, the niche-based arguments advanced for positive local diversity-functioning relations can, with appropriate modifications, also be advanced for a positive relation between diversity and ecosystem resilience at the landscape scale.

In reality, little is actually known about the effects of large-scale diversity losses on ecosystem processes and services. It has been hypothesized that observed declines in pollinator and natural enemy diversity in intensively managed agricultural landscapes could result in less efficient delivery of the ecosystem services crop pollination and biological control of pests (Buchman and Nabhan 1996; Daily 1997; Björklund *et al.* 1999). However, relevant data collected at the relevant scales are largely lacking. Since designing and performing classical experiments at the landscape and regional scales is difficult, to say the least, other means must be used to obtain knowledge on large-scale effects of biodiversity loss on ecosystems.

One way of dealing with this problem is to construct model ecosystems to examine how landscape structure may affect species distributions and diversity (Gonzalez *et al.* 1998). The microcosm approaches of McGrady-Steed *et al.* (1997) and Naeem *et al.* (2000a) could also be extended by using microcosms connected to each other in various ways to mimic variation in landscape configuration (cf e.g. Holyoak 2000).

Apart from such model ecosystem studies, the closest we have to large-scale field experiments is probably the comparison of lands under different management practices, natural landscape differences, natural gradients or areas with different restoration methods. For example, Östman *et al.* (2001) studied the efficacy of biological control and patterns of diversity in paired organic (pesticide-free) and conventional farms along a gradient of landscape heterogeneity. In this case, the ecosystem service of biological control was enhanced in landscapes that are more heterogeneous and on organic farms. However, there was no obvious connection to the diversity of natural enemies, which was higher in heterogeneous landscapes but surprisingly, lower for carabids on organic farms.

To summarize, processes affecting regional diversity patterns will often interact with local processes to produce local relationships between diversity and rates of ecosystem processes. Even if no clear diversity-functioning relation (positive or negative) can be found locally, regional diversity can still be an important determinant of ecosystem processes at local sites. This may be self-evident for many researchers studying ecosystems and population dynamics at larger scales, but knowledge of large-scale processes still needs to be actively incorporated into studies of diversity and ecosystem functioning.

18.5 The way forward

It is unlikely that scaling problems will be easily solved. However, it should be possible for ecologists to provide better guidelines for scaling issues than they do at present. We still lack a comprehensive treatise on scales in ecology (Bengtsson 2000 reviewing Peterson and Parker 1998) that could help us. What can be done in the meantime?

Firstly, more studies should not only repeat the same approach at different sites (cf Hector *et al.* 1999) but also at different spatial scales, for example conducting the same diversity treatments in nested experiments. Studies scaling up from local plots to incorporate interactions between local, landscape, and regional diversity, and the ensuing effects on ecosystem functioning, are critically needed.

A drawback of most field studies is their short duration relative to the dynamics of organisms and processes affecting community composition. Some microcosm studies have attempted to ameliorate this situation (McGrady-Steed *et al.* 1997; Naeem and Li 1997; Naeem *et al.* 2000; see Petchey *et al.*, Chapter 11). However, these systems still have to be scaled up to larger spatio–temporal scales, which is by no means easy. Moreover, there is a general, but perhaps unfounded, scepticism to microcosm studies among many ecologists. This means that microcosm studies at best can be used to complement other approaches. Long-term studies that simultaneously examine how community structure and processes change through time will be informative in this respect.

Clever and innovative use of natural experiments and gradients, variation in management practices, and restoration projects to examine hypotheses at

landscape and regional scales should increase. For example, analysis of diversity–ecosystem functioning relationships in woody ecosystems could be conducted by well-planned observational studies (Troumbis and Memtsas 2000). Effects of regional variation in diversity on other important ecosystem services than biomass production should be of high priority, e.g. nutrient retention, pollination and biological control. More fundamentally, we need a better understanding of how regional diversity influences local diversity in different ecosystems.

At the same time, studies on larger scales necessarily have drawbacks. They need to be complemented by in-depth studies of mechanisms, and these will have to be performed at smaller scales. The degree of replication and control over treatments in large-scale studies will be lower than in most experimental studies. Requirements on statistics and methodology may have to be relaxed (but not abandoned) since control of all confounding factors is impossible. In some cases designs such as BACI (before-after-control-impact) as used in whole-lake manipulations (e.g. Carpenter and Kitchell 1993) will be useful. Because spatial and temporal scales are related, large-scale studies will usually take more time. Hence, reliable results will take some time to obtain, which must be acknowledged. On the other hand, the issues are so pressing that it is impossible to wait until the last sceptic is convinced, before results are used for management and policy.

Theories and model systems that explicitly incorporate several scales are also needed. In order to be helpful for empirical studies, new theory should be developed that incorporates local–regional interactions and generates hypotheses for larger scales than local plots. Then we may ultimately be able to answer whether diversity really is important for the resilience and maintenance of ecosystem services at larger scales in space and time.

18.6 Conclusions

Scaling effects of biodiversity on ecosystem functioning presents problems that need to be solved by both empirical and theoretical studies performed at several scales simultaneously. Species loss at a regional scale may result in each local site not receiving the set of species necessary to realize the potential rate of ecosystem processes such as productivity. We suggest that at local sites, the main effects of diversity are on rates of ecosystem processes, but at a regional scale diversity will mainly influence resilience and stability-related functions. Diversity effects on functioning may or may not be similar across ecosystem types, depending on the process and nature of the system. When systems are driven by disturbances, top-down regulation or interference competition, positive diversity–ecosystem functioning relations may be less common. In contrast, systems with exploitative competition and resource partitioning are most likely to show positive effects of diversity on ecosystem functioning. Studies in different ecosystems examining diversity–ecosystem functioning relations at local, landscape, and regional scales are needed. A better theoretical understanding of the relationships between regional and local diversity will be helpful when interpreting such results. In the absence of true large-scale experiments, we advocate more clever and innovative use of natural experiments, diversity gradients, and managed systems.

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